

FISH COMMUNITY STRUCTURE IN DRY-SEASON STREAM POOLS¹

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Abstract. Fish assemblage patterns were examined in 40 dry-season pools in a hydrologically variable river drainage in northeast Texas, to test the hypothesis that fish assemblage structure is correlated with environmental gradients of habitat characteristics. The study focused on two questions: 1. Do discrete, identifiable fish assemblage patterns exist? 2. If so, how are they related to environmental conditions?

The null hypothesis that fishes were randomly distributed among pools was rejected, indicating that assemblage patterns existed. Cluster analyses of the relative abundance of fish species detected three fish assemblages dominated by: mosquitofish; black bullhead; and sunfish-shiner-mosquitofish. Factor analysis reduced environmental variables to six factors representing pool depth, pool persistence, channel size, canopy cover, pool substrate, and pH, by which assemblages could be discriminated. These results demonstrated a relation between fish assemblage structure and environmental conditions in the pools. The discriminating variables varied along a gradient, and fish assemblages varied similarly. The study supported model predictions for gradient trends in species richness, species composition, fish size, and fish density, but not for species density.

Key words: *community structure; environmental variability; fish assemblages; null models; streams; Texas.*

INTRODUCTION

Although assessment of the existence and cause of biological structure is difficult in many animal communities (Sousa 1984, Strong et al. 1984), recent studies have suggested that fish assemblages in variable environments may provide appropriate test systems (Matthews and Heins 1987, Schlosser 1987). Schlosser (1987, Schlosser and Toth 1984) found that small minnows dominated in the shallowest reaches of small warmwater streams but, as temporal stability and habitat heterogeneity increased downstream, minnow abundance decreased while sucker and sunfish abundance increased. Based on such observations Schlosser (1987) proposed a model (Fig. 1) predicting variation in fish communities along physical stream gradients of shallow and variable to deep and stable.

Fish assemblages are structured (in species composition) by biotic factors, such as competition (Grossman 1982, Ross et al. 1985) and predation (Cerri and Fraser 1983, Werner et al. 1983, Moyle and Vondracek 1985, Power 1984, 1987), and by physical factors, such as habitat diversity (Gorman and Karr 1978), physicochemical gradients (Kushlan 1976, Matthews and Styron 1981, Tonn and Magnuson 1982, Rahel 1984),

and flow regime and channel morphology (Harrell 1978, Horwitz 1978, Schlosser 1985). However, environmental variability may also inhibit formation of persistent, repeatable assemblages (Grossman et al. 1982, Sale and Douglas 1984).

Physical factors appear to be more important in structuring assemblages in variable environments, including marshes (Kushlan 1976), streams (Harrell 1978, Matthews and Styron 1981), and lakes (Tonn and Magnuson 1982). Schlosser's (1982, 1985) studies of unstable streams suggest that physical characteristics influence assemblage organization through reproductive success and recolonization rates. Biotic interactions appear to be more important in stable environments (Grossman 1982, Schlosser 1982, Moyle and Vondracek 1985, Ross et al. 1985).

Influenced by the results of these studies, we examined the generalizations of Schlosser's (1987) model in an intermittent warmwater stream, testing the null hypothesis that no relationship exists between environmental characteristics of dry-season pools and the structure of the fish assemblages found there.

Before considering this matter, we asked whether discrete, identifiable patterns actually existed among pool fish assemblages, to consider the role that chance could play in creating the appearance of patterns (Conner and Simberloff 1979, Jefferies 1989), by comparing the observed pattern to random expectations generated by a neutral (null) model (Caswell 1976, Strong et al. 1979, Matthews 1982). Our models tested the existence of nonrandom patterns without implying causal mech-

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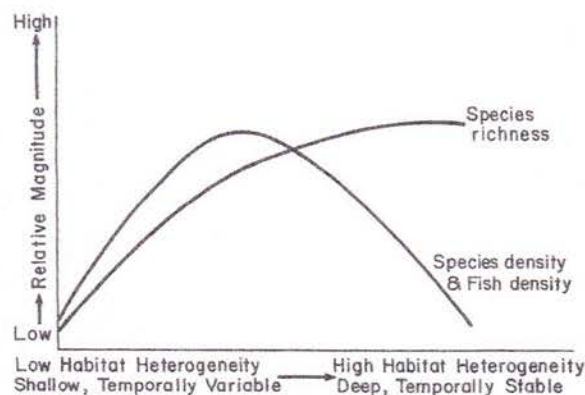


FIG. 1. Hypothetical model of fish community attributes along a gradient of increasing habitat heterogeneity and pool development in small warmwater streams (based on Schlosser 1987).

animals (see Matthews 1982 or Roughgarden 1983), and therefore were not biased by the implicit biological and causal assumptions associated with any model (Schoener 1987). We also considered the effects of data selection on the identification of assemblage patterns.

STUDY AREA

We studied pools in 12 channels of the Sulphur River (northeast Texas, USA). Precipitation (112 cm annually) is seasonal; the wettest months are April and May and the driest July and August. Stream flow is similarly seasonal. Flow ceases in summer and in the winter. As water levels fluctuate, isolated pools form in the streambed. The study sites experienced up to 15 drydowns per year.

Fishes become concentrated in pools as the water recedes. Each pool has a similar array of potential colonists, but pool characteristics differ. These isolated dry season pools provide communities with well-defined boundaries. All fishes can be removed, eliminating the sampling errors that have complicated interpretation of previous fish assemblage studies (Grossman et al. 1982, Herbold 1984, Rahel et al. 1984, Ross et al. 1985).

METHODS

Forty dry-season pools were chosen to maximize heterogeneity among sites. Pools were sampled as soon as possible after they became isolated in the major annual dry periods of 30 July–26 August 1986 and 23 June–30 July 1987. Pools were monitored until flow returned. Fish were removed by electroshocking, seines (0.32-cm² mesh), dip nets, and rotenone (at two deep sites). The effectiveness of physical removal (electroshock/seine/dip net) was checked at four sites by subsequent rotenone applications. At least 95% of the fish had been removed, missing only small (<1.2-cm) individuals of the two most abundant species (*Gambusia affinis*, *Lepomis cyanellus*).

Before fish sampling, 18 environmental character-

istics were measured in each pool: (1) oxygen (fixed in the field, titrated same day, modified Winkler micro-method, mg/L), (2) turbidity (measured same day sampled, Hach DR-EL/1 water analysis kit, JTU), (3) conductivity (measured same day sampled, Hach model 17250 Mini Conductivity Meter, $\mu\text{S}/\text{cm}$), (4) pH (measured on site, ColorpHast pH strips); (5) channel width (center of pool to the nearest bank, cm), (6) channel depth (from the high-water mark to bed, cm), (7) pool surface area (longest axis by width, measured at 1-m intervals perpendicular to long axis), (8) average pool depth (mean of 10 random depth measurements, mm), (9) maximum pool depth (mm), (10) water temperature, (11) aquatic vegetation (presence or absence), (12) substrate type (percent covered by nonsediment [sediment = particles <0.47 cm diameter; sediment cover = 100 - sum of percentage cover of nonsediment particles]. Nonsediment categories included boulders [≥ 30 cm], rubble [7.6–29.9 cm], and gravel [0.47–7.59 cm]), (13) distance to nearest pool (cm), (14) percent covered by canopy, (15) habitat diversity (mean of the ratio of the distance recorded by a tape measure laid in contact with the bottom along the length and widths of each pool to the straight-line distance of each length and width transect), (16) stream order (Strahler 1957), (17) distance of pool from permanent water (from United States Geological Survey topographic quadrangle maps), and (18) persistence (number of days each site was wet between 1 June and return to flow each year). Samples from both years were combined since "year" did not load as a stepwise discriminating variable, nor were assemblage patterns separable on the basis of year or date.

We tested the null hypothesis that fishes were randomly distributed among pools by comparing the actual distribution against two neutral models. Model 1: Given a known distribution of the numbers of each species collected, each individual fish was randomly reassigned to a pool; column totals (total number of each species collected) remained constant. Model 2: Given a known distribution of both the numbers of each species collected and the total number of fish found in each pool, each individual fish was randomly reassigned to a pool; the number of fish that could be reassigned to a pool was limited to the number that actually occurred; column and row totals remained constant. One hundred random permutations of each model were generated and the chi-square of each was calculated. This resulted in a chi-square frequency distribution for both of the randomly generated models to which the observed chi-square value was compared. If the observed value fell in the critical region (0.02) of the distribution we rejected the null hypothesis (random assemblage structure) since the probability of obtaining an observation equally or more deviant than the observed value was less than the significance level (randomization test, Sokal and Rohlf 1981:788). Permutations were run using QuickBasic.

Fish density (number of fish per square metre), species richness (number of species), and species density (number of species per square metre) were calculated. The abundance of each species was converted to relative abundance (percent of total) and transformed to octave scale (Gauch 1982). Percent canopy cover and percent substrate cover were arcsine transformed; other continuous environmental variables, except pH, were log transformed. Group comparisons were made using ANOVA (SPSS 1983), $\alpha = .05$. Fish assemblage patterns were identified using cluster analysis (CLUSTER procedure, SPSS 1983) for the two primary data sets (presence/absence and octave-transformed relative abundances) and for octave-transformed relative abundance data for the five most common species (mosquitofish [*Gambusia affinis*], green sunfish [*Lepomis cyanellus*], golden shiner [*Notemigonus crysoleucas*], black bullhead [*Ictalurus melas*], and bluegill [*Lepomis macrochirus*]) and for the remaining "rare" species together. Each analysis included all 40 pools.

Relationships among fish assemblages and environmental parameters were evaluated using discriminant function analysis (DISCRIMINANT procedure, direct method, SPSS 1983). Cluster membership was the grouping variable and environmental variables the predictor variables.

To reduce the number of variables (and to account for autocorrelation), factor analysis (FACTOR procedure, SPSS 1986) of the 18 environmental variables was performed (Green 1979, Williams 1983). Factor scores were then used as the predictor variables in a second discriminant function analysis of cluster membership. Since classification accuracy in discriminant analysis is overestimated when the same cases used to derive the function are classified (Klecka 1980), jackknifed analyses were performed. The expected and observed frequencies of correctly classified jackknifed results were compared by chi-square.

RESULTS

Richness, density, length

We collected 23 of the 83 fish species reported for the Sulphur River Basin (Ingold 1977). Species composition varied; three species (green sunfish, mosquitofish, and golden shiner) were found in more than half the pools. Twenty-nine pools (72%) held five or fewer species; all but four pools had fewer than 10. Half the pools (21) had a fish density of 10 or fewer fish/m²; two pools had a density > 100 fish/m². Ninety-six percent of the fish were < 5.0 cm long; the largest proportion of these (40%) were in the 1.1–2.0 cm size class.

Species abundance

The five most abundant species (mosquitofish, green sunfish, golden shiner, bluegill, and black bullhead) comprised 97% of all fish sampled. The percent composition of mosquitofish and the percent composition

of sunfish and bullheads were negatively correlated among pools ($r = -0.72$, $P < .05$). The randomization tests revealed that the chi-square of the observed abundance distribution of fishes differed significantly from that of both neutral models ($P < .02$), suggesting that the pattern of relative fish abundances was not random.

Assemblage structure

Based on species presence/absence data, two fish assemblage groups were identified (Fig. 2). The four pools in the second cluster had a higher species richness (10–16 species). Relative abundances clustered into three assemblage groups (Fig. 3). The first group (30 pools) had relatively equal numbers of green sunfish, golden shiners, and mosquitofish. In the second group (6 pools), mosquitofish predominated without large numbers of green sunfish or golden shiners being present. In both these groups of pools, no other species made up > 10% of the fish present. Pools in the third group (4 pools) had relatively few mosquitofish, green sunfish, and golden shiners. In these pools black bullheads predominated and one also contained a relatively large number of bluegills.

Cluster analysis of the relative abundance of only the five most abundant fishes yielded identical results to cluster analysis based on the relative abundance of all the species, except for one pool. Thus, the absence of the rarer species did not change assemblage group classification. The cluster analysis of "rare" species alone revealed no pattern.

Cluster analysis of the relative abundances of all species provided a finer resolution of assemblage pattern than did presence/absence data. Presence/absence analysis failed to distinguish between a mosquitofish group and sunfish–shiner–mosquitofish group. In subsequent analyses we use the three groups (sunfish–shiner–mosquitofish, SSM; mosquitofish, MOF; bullhead, BUL) identified by analysis of octave-transformed relative species abundances.

Once identified, the three groups can be characterized by other attributes (Fig. 4). The mean species richness was significantly different among the three fish assemblage groups, lowest in the MOF pools, and highest in the BUL pools. Fish sizes showed a species effect and differed significantly among groups. Mean fish densities and species densities were not significantly different among groups. However, a trend of decreasing fish density was evident as species richness and fish length increased (Fig. 4).

Environmental variables

All pools were located in first-, second-, or third-order streams. Pools ranged from 3.2 to 235 cm deep, and 12–4324 m² in surface area. Oxygen concentrations were 1.58 to 7.60 mg/L (anaerobic pools were not sampled as they had no fish). Conductivity and turbidity were generally low (300–700 μ S, 3–500 JTU) and pH was low (except for site 11, where pH = 8.8).

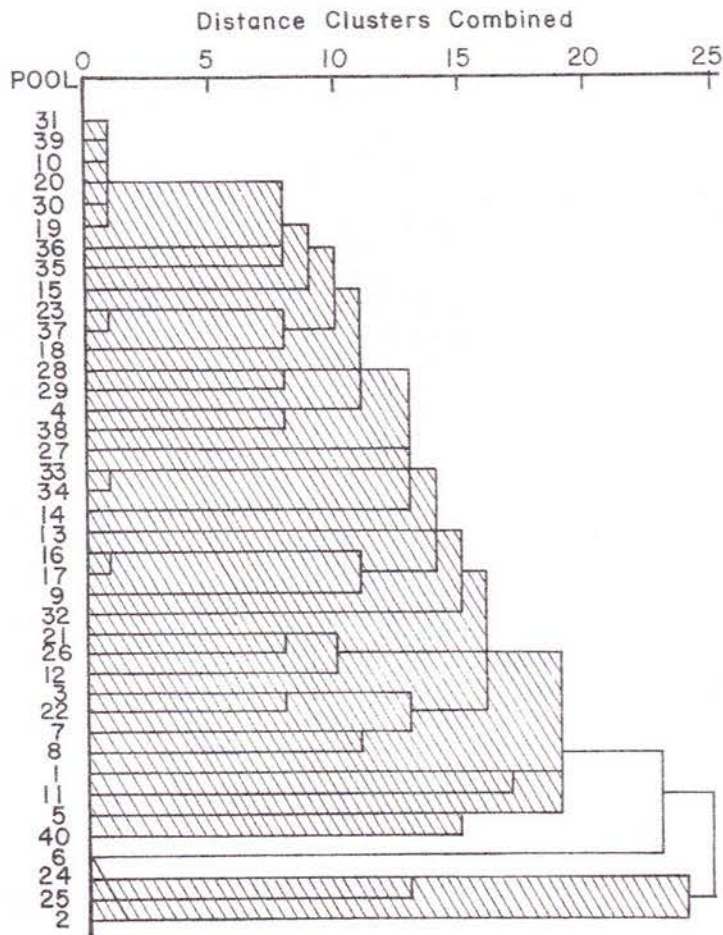


FIG. 2. Dendrogram showing the two groups revealed by a cluster analysis (pools 6, 24, 25, 2 in higher species richness group, remaining pools in most abundant species group) based on fish species presence/absence. The position of the horizontal line on the distance axis indicates the scaled distance at which clusters (pools) were combined.

Habitat diversity was lowest in the two deepest pools (0.836–1.220). Isolation varied from a few centimetres to 100 m. The least persistent pools were wet for only 40 d after 1 June; 11 pools persisted through the summer. Most pools persisted 75–85 d before drying. Distance to permanent water ranged from 1 to 26 km.

A factor analysis extracted six factors with eigenvalues > 1 , which together accounted for 76.7% of the variance among sites. Each factor is interpretable biologically (Table 1).

Environmental correlates

Means for the environmental variables grouped according to fish assemblage type (MOF, SSM, BUL) are positioned along an environmental gradient (Fig. 4). Variables describing depth, persistence, and habitat diversity were significantly different among groups (Fig. 4). MOF pools were shallowest, least persistent, in the smallest channels, and were farthest from permanent water and from other pools. BUL pools were deepest, most persistent, in the largest channels, least habitat

diverse, and were closest to permanent water. SSM pools had intermediate values for depth, persistence, channel size, distance to permanent water, and had the largest pool surface areas. Physical differences among pool groups varied along a gradient of increasing pool depth, channel size, and persistence, and of decreasing within-pool habitat diversity.

The three fish assemblage groups could be discriminated at 100% accuracy on the basis of the original 18 environmental variables (Fig. 5, Table 2). Environmental variables providing the best discrimination among groups (having the highest correlation with the two canonical discriminant functions) included days wet, average depth, maximum depth, pool area, and bank height. Discriminant analysis of the six environmental factors produced similar but less definitive separation of groups (85% correct classification) (Fig. 5, Table 3). "Jackknife" validation showed a classification rate of 70%, which was significantly different than the expected classification rate due to chance alone ($\chi^2 = 29.9$, $df = 1$, $P < .05$). Depth, persistence, and chan-

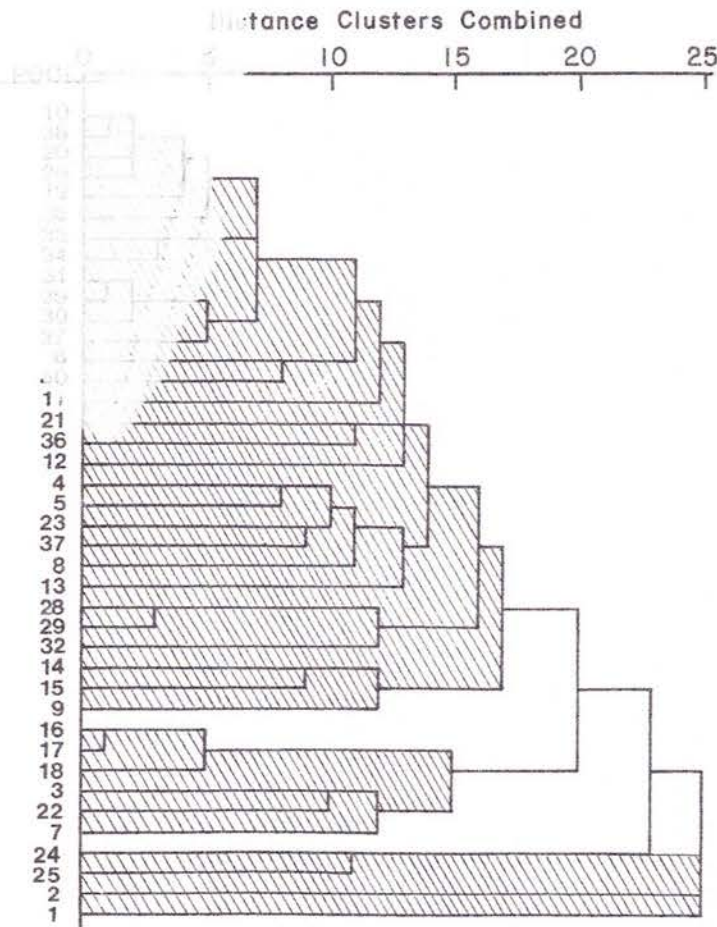


FIG. 3. Dendrogram showing three groups based on cluster analysis of octave-transformed relative fish species abundance data. The position of the horizontal line on the distance axis denotes scaled distance at which clusters were combined.

nel and pool size factors were again the best discriminators between groups (Table 3).

DISCUSSION

Assemblage structure

Fish assemblage patterns exist in drying pools and can be delineated. Fish species were distributed non-randomly among drying pools, and three fish assemblage groups were identified based on relative abundances. The enhanced resolution of relative abundance data (contrasted with presence/absence data) appears to derive from its additional information content. Similar findings were reported in Oklahoma streams (Smith and Powell 1971, Echelle and Schnell 1976).

That elimination of rare species had no effect on identification of assemblage groups (based on relative abundances) suggests that rare species can be deleted from community analysis without biasing pattern detection, confirming suggestions of Green (1979) and Gauch (1982). It remains appropriate to test the impact of rare species deletion in each study before their ex-

clusion. Because our data were based on complete removal and therefore were unbiased with respect to rare species, we included all species in our analysis.

Test of the stream gradient model

Except for species density, our results support the conceptual framework of stream fish community structure proposed by Schlosser (1982, 1987) (Fig. 1) and in addition provide quantitative information about variation in relative size and abundances (Fig. 4). Species richness was hypothesized to increase in small, warmwater streams as depth, habitat heterogeneity, and temporal stability increased down-gradient. The species richness in our dry-season pools showed this trend, increasing as pool depth, pool persistence, and channel size increased. Fish density was hypothesized to peak at an intermediate level and then decrease down-gradient as fish species composition shifted from large numbers of small fishes to fewer, larger fishes. This appears to be the case in our pools as well. While it is not clear just where fish densities reach their highest level (MOF or SSM pools), they do exhibit the

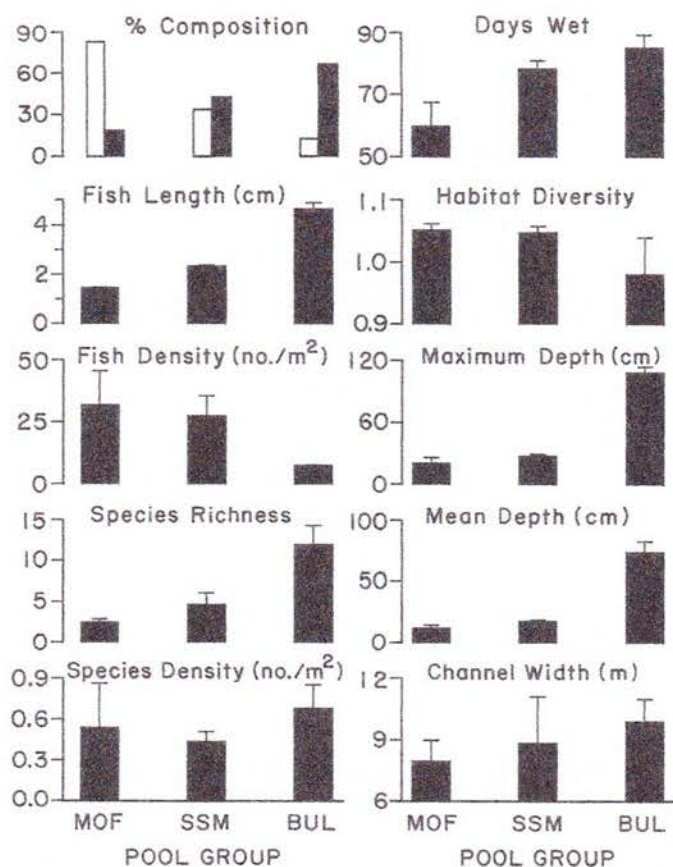


FIG. 4. Plots indicating that the Sulphur River pools are located along a gradient of increasing pool depth, pool persistence (days wet), channel size, and decreasing within-pool habitat diversity. Mean and SE are shown for each variable as it relates to the three pool fish assemblage groups (MOF = mosquitofish, SSM = sunfish-shiner-mosquitofish, BUL = bullhead). Pool groups represent fish assemblage clusters grouped on the basis of differences in the relative abundances of species. Fish length, fish density, and species composition also change in relation to the gradient. Percent species composition is expressed in terms of mosquitofish (open bar) and sunfish-bullhead (solid bar) abundance.

TABLE 1. Factor loadings for each environmental variable (only loadings >0.40 are reported).

Variable	Factors					
	Channel size	Canopy cover	Pool depth	Pool pH	Persistence	Substrate
Stream order	.85					
Bank height	.81					
Channel width	.73	-.45				
Conductivity	.67					
Permanent water	-.56			-.67		
Nearest pool	.48				-.48	
Habitat diversity	-.40					
Temperature		-.81				
Canopy cover		.77				
Turbidity		.69				
Oxygen concentration		-.60	-.53			
Aquatic vegetation		.57				
Pool area		-.43	.54			
Average depth			.94			
Maximum depth			.90			
Pool pH				.90		
Days wet					.86	
Substrate not sediment						.89

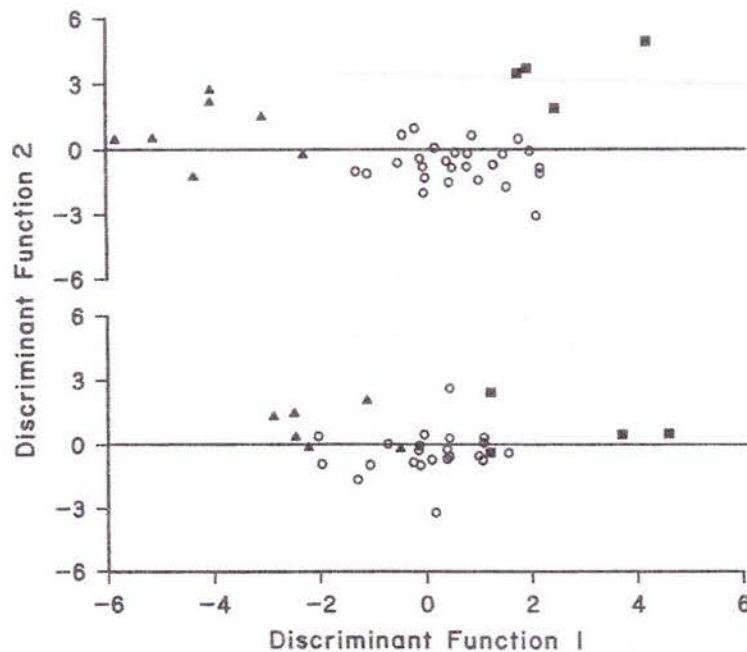


FIG. 5. Scatterplot of the discriminant scores from the discriminant function analyses (DFA) of the original 18 environmental variables (top) and the six factors extracted by factor analysis (bottom). Correlations of the variables with each discriminant function can be found in Tables 2 and 3. Each pool is denoted by a symbol representing its fish assemblage group (triangle = MOF, circle = SSM, square = BUL). Pools with the same discriminant score are represented by only one point. DFA of the 18 environmental variables correctly classified all pools. The DFA of the six factor scores shows that while three cases were misclassified, discrimination among groups is still possible.

predicted peak at intermediate pool characteristics and decline where pools are deeper, larger, and more persistent (Fig. 4).

The model likewise hypothesized that species density will peak at some point and then decrease down-gradient, but this was not the case in the Sulphur River

pools. Unlike fish density and species richness, species density showed no trend in relation to the environmental gradient (Fig. 4). Three explanations present themselves. The first is a question of sample size: the seven pools in the MOF group and the four pools in the BUL group have large standard errors. Second, species density may not be related to the physical gradient in Sulphur River pools in the same way as in Illinois streams. Much of the variation in species density in Schlosser's model was a result of between-season differences in juvenile recruitment, colonization, and age/size classes. Temporal variability was not a part of our study. Finally, Texas stream pools may represent the extreme left of the hypothesized model, and thus the apparent increasing trend in species density along

TABLE 2. Pooled within-groups correlations between discriminating environmental variables and the two canonical discriminant functions.

Variable	DF 1 correlation	DF 2 correlation
Days wet	0.23935*	0.06424
Aquatic vegetation	0.14992*	-0.05010
Nearest pool	0.08696*	0.07176
Pool area	0.08613*	0.04495
Permanent water	-0.08513*	0.01674
Turbidity	-0.04679*	0.04368
Average depth	0.15931	0.36012*
Maximum depth	0.18184	0.33359*
Oxygen concentration	-0.21853	-0.32843*
Bank height	0.00390	0.28573*
Habitat diversity	0.05613	-0.28315*
Stream order	-0.04076	0.20811*
Temperature	-0.08577	-0.18685*
Channel width	-0.05129	0.15415*
Substrate	-0.08522	0.14637*
Conductivity	0.07967	-0.11565*
pH	-0.00032	-0.03861*
Canopy cover	-0.00375	0.03711*

* Within each discriminant function, the significant correlations are listed in order of decreasing magnitude.

TABLE 3. Pooled within-groups correlations between discriminating factors and the two canonical discriminant functions.

Factor	DF 1 correlation	DF 2 correlation
Pool depth	0.65191*	0.24699
Canopy cover	0.22268*	-0.01646
Substrate	-0.04796	0.62494*
Persistence	0.26353	-0.49447*
Pool pH	0.06985	-0.34882*
Channel size	0.22654	0.31820*

* Within each discriminant function, the significant correlations are listed in order of decreasing magnitude.

the gradient would be in agreement with model predictions for that part of the gradient.

Schlosser found that the age/size structure, species composition, and trophic structure of fish communities in Illinois streams shifted from dominance by relatively large numbers of small species (minnows), toward fewer, larger predatory species (sunfish) as depth, temporal stability, and habitat heterogeneity increased. This shift was evident in our pools in relation to similar physical stream characteristics, and is further demonstrated by the significant negative association between mosquitofish abundance and the abundances of larger sunfish and bullheads. Several distinctions between the model and our results are attributable to the systemic differences between Illinois streams and dry-season pools in warmwater Texas streams. In our study system, pool persistence and isolation, rather than temporal stability (*sensu* Schlosser 1987), were used to measure pool stability. Also, in Texas, habitat heterogeneity did not increase downstream. Schlosser, studying permanent streams, evaluated habitat heterogeneity in terms of depth, current, and channel substrate. In our study, habitat heterogeneity was a within-pool measurement of substrate roughness.

Environmental correlates of assemblage structure

The five most common fishes found in Sulphur River pools are tolerant of high temperatures, low oxygen levels, and rapid changes in these factors (Carlander 1973, Scott and Crossman 1973). During summer drought, temperature and water levels in shallow pools vary widely. Photosynthesis and respiration quickly change pH and dissolved oxygen levels. Sulphur River fish assemblage groups appear to reflect, in part, susceptibility to harsh conditions. Analogous assemblages of tolerant species have also been reported for variable warmwater streams elsewhere (Echelle et al. 1972, Echelle and Schnell 1976, Matthews and Hill 1980, Matthews and Styron 1981, Rose and Echelle 1981, Ross et al. 1985). In these streams, as predicted by the stream gradient model, smaller, more tolerant species are abundant in the shallower, more variable headwaters. Less tolerant, "pool" species occurred in deeper, less variable downstream reaches. Patterns such as these reflect dispersal and segregation during relatively mild conditions and convergence to appropriate habitats when conditions turn rigorous (Matthews and Hill 1980, Ross et al. 1985).

Green sunfish, golden shiners (in our study most abundant in pools of intermediate depth and persistence), and mosquitofish are "pioneer species," capable of surviving harsh conditions and of invading areas having low populations of other species. Green sunfish are usually rare in habitats that contain more than three or four other species, and are poor competitors (Moyle 1976). Thus in Sulphur River pools, green sunfish occurred where only a few other "pioneering" species could survive and biotic interaction was probably not

as intense as in the deeper, more persistent and species-rich pools. Moyle and Nichols (1973) and Echelle and Schnell (1976) found similar patterns for relative abundances of green sunfish and golden shiners in small, intermittent streams. The model predicts that the fish predominant in shallow, temporally variable habitats in small, warmwater streams will be "colonizing" species (Schlosser 1987). Livebearing mosquitofish, which predominated in the shallowest, least persistent headwater pools of the Sulphur River Basin, are even better colonizers than the minnows and shiners found in Schlosser's streams (Kushlan 1980, Brown 1985, Kennedy et al. 1986, Robbins et al. 1987). Small fishes, such as minnows and mosquitofish, may be restricted to spatially isolated, shallow refugia because of predation losses in deeper areas (Schlosser 1987). That predation secondarily mediates fish community structure has been demonstrated or suggested elsewhere (Kushlan 1976, Moyle and Li 1979, Fraser and Cerri 1982, Power and Matthews 1983, Werner et al. 1983, Fraser and Emmons 1984, Power 1984, 1987). Persistent pools may provide a refuge from harsh environmental conditions, permitting the survival of larger predatory fish there (Tonn and Magnuson 1982, Rahel 1984, Schlosser 1987). Clearly, summer harshness and rapid environmental changes during flood or drought limit colonization or persistence of larger, less tolerant species in Texas, Virginia, and Oklahoma streams (Harrell 1978, Matthews and Hill 1980, Matthews and Styron 1981, Power 1984, 1987, Ross et al. 1985).

Pool persistence was an important discriminating variable among fish assemblage groups in this study, and the risk associated with drying pools is a measure of environmental harshness in the Sulphur River. No fish kills were observed in our study pools prior to their actually drying. All but one of the MOF pools dried completely before the return of flow. Six of the SSM pools persisted through the summer, and those that dried did so in the last few days of the dry season. Pool persistence of 80–85 d would result in survival through the summer drydown in most years.

Thus, factors affecting abundances are likely a balance between predation risks within the pool and the increased habitat harshness of drying pools. The most persistent pools supported larger predatory fish and had relatively little habitat complexity for smaller prey fishes. Chances of survival for most smaller fish were best in intermediate pools, which had fewer predators and interspecific competitors, more habitat heterogeneity, and a relatively good chance to persist throughout the summer. Mosquitofish almost alone dominated pools that were too harsh for most other species.

Considering the stream fish community as a whole, the development of larger, deeper pools along a physical gradient in small variable streams would increase the complexity of regulators of community structure, both within and among pools. Our results support the view that populations of small, colonizing fish species

may be enhanced by environmental disturbance caused by flow regime fluctuations and by the presence of refugia, whereas competition and habitat-related differences in foraging efficiency may have greater influence on larger fishes that survive in deep pools.

CONCLUSION

Our results support the hypotheses that fish assemblage patterns exist and can be predictably related to a physical gradient of depth and persistence in small, warmwater streams. Furthermore, although data selection can substantially affect the outcome of community analyses, patterns can be predictably related to environmental correlates. The factors regulating fish assemblage structure may differ in relation to environmental variability. Physical processes (stream morphology and highly unstable, temporally variable stream flows) appear to be more important regulators of stream pool fish assemblage structure among pools, than are factors such as fish predation and competitive interactions, which may be more important as within-pool regulators of fish community structure.

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